

# The Asia-to-America Influx of Avian Influenza Wild Bird Hosts Is Large

Kevin Winker<sup>A</sup> and Daniel D. Gibson

University of Alaska Museum, 907 Yukon Drive, Fairbanks, AK 99775

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**SUMMARY.** Recent literature has underestimated the number and taxonomic diversity of wild birds moving between Asia and North America. Our analyses of the major avian influenza (AI) host groups show that fully 33 species of waterfowl (Anatidae), 46 species of shorebirds (Charadriidae and Scolopacidae), and 15 species of gulls and terns (Laridae) are involved in movements from Asia to Alaska across northern oceans (Table 1). Our data suggest that about 1.5–2.9 million individuals in these important host groups move from Asia to Alaska annually. Among all of the host groups we consider most relevant for AI virus movement models in this region (waterfowl, shorebirds, and gulls and terns), it seems likely that thousands of AI-infectious birds may be involved in annual Asia-to-America migrations. Importantly, host availability in Alaska once these vectors arrive is also very high, representing at least 5–10 times more birds and infectious birds than the host populations moving from Asia to North America. Incorporating our data into a recent model of the global spread of the highly pathogenic H5N1 suggests that wild birds are a more likely source of this strain being brought into the United States than trade in domestic birds, although the latter remain a numerically more probable source of introduction into the New World. Our results should help in defining the key taxonomic, geographic, and seasonal factors involved in this complex intercontinental association of wild bird AI hosts. The next steps are to determine infection rates of low pathogenicity and highly pathogenic viruses among these hosts and to incorporate these into dynamic models.

**RESUMEN.** La movilización de aves silvestres hospedadoras del virus de la influenza de Asia hacia America es importante.

La literatura reciente ha subestimado el número y la diversidad taxonómica de las aves silvestres que se movilizan entre Asia y America del Norte. El análisis de los principales grupos hospedadores de influenza aviar, muestra que 33 especies de aves acuáticas (*Anatidae*) 46 especies de aves costeras (*Charadriidae* y *Scolopacidae*) y 15 especies de gaviotas y charranes (*Laridae*) están relacionadas con los movimientos desde Asia hasta Alaska a través de los Océanos del Norte. Los datos obtenidos sugieren que entre 1.5 y 2.9 millones de individuos pertenecientes a estos importantes grupos se movilizan anualmente desde Asia hasta Alaska. Entre todos los grupos de hospedadores que se consideraron de mayor relevancia para los modelos de movimiento del virus de influenza aviar en esta región (ave acuáticas, costeras y gaviotas), parece probable que miles de aves infectadas con influenza aviar estén relacionadas con migraciones de Asia hacia America. Es importante mencionar que la disponibilidad de hospedadores en Alaska una vez que estos vectores llegan es muy alta, representando al menos 5 a 10 veces más aves y aves infecciosas que las poblaciones de hospedadores que migran desde Asia hasta Norte America. La incorporación de la presente información en un modelo reciente sobre la diseminación global del virus de la influenza aviar de alta patogenicidad H5N1, sugiere que las aves silvestres son una fuente más probable de introducción de estas cepas a los Estados Unidos que el comercio de aves domesticas, aun cuando el comercio de aves domésticas se mantiene como una fuente numéricamente mas probable para la introducción del virus al nuevo mundo. Estos resultados deben ayudar en la identificación de los factores taxonómicos, geográficos y estacionales que son clave y que están asociados con la compleja interacción intercontinental de las aves silvestres hospedadoras de influenza aviar. Los siguientes pasos son la determinación de los porcentajes de virus de baja y alta patogenicidad entre estos hospedadores y la incorporación de estos datos en modelos dinámicos.

Key words: avian influenza virus, avian migration, intercontinental disease transport, models

Abbreviations: AI = avian influenza; HP = highly pathogenic; LP = low pathogenicity

Efforts to understand the global movements of avian influenza (AI) virus have consistently tended to underestimate the number and diversity of wild bird hosts coming to the Americas from Asia. Researchers from various fields have inadvertently underrepresented the importance of wild bird movements between Asia and the Americas (4,10,17,29,34). In considering AI movements in wild bird hosts, Donis *et al.* (10) suggested that waterfowl movements across the Pacific Ocean were minimal, and Kilpatrick *et al.* (17) provided an Asia-to-America wild bird movement factor fully three orders of magnitude smaller than we think appropriate for general AI models.

This inadvertent underrepresentation of bird movements between Asia and North America may stem from the largely Atlantic-centric perspective of Western science and the longstanding political divides among northern Pacific Rim countries. Bird research and the reports thereof tend to stop at the edges of maps and country boundaries,

and the Alaska migration system, one of the most global in scope, is also one of the last on earth to be fully described. The fact is that large numbers of wild birds, potential hosts of AI virus, cross from west to east each year from Asia to North America (and vice versa) across the North Pacific and Arctic oceans, and a full understanding of the global movements of AI virus requires that these hosts be appropriately incorporated into avian influenza research programs and models. The need to properly account for the magnitude of this host movement system antedates the emergence of the currently circulating highly pathogenic (HP) H5N1, and this need remains whether one is considering the potential movements of all AI viruses (low pathogenicity [LP] or HP) or of only a specific strain or gene lineage. Here we provide quantified taxonomic and numeric estimates for wild bird movements between Asia and Alaska in the groups of birds from this region that are probably the most important as AI virus hosts: waterfowl (Anatidae), shorebirds (Charadriidae and Scolopacidae), and gulls and terns (Laridae). Insofar as Alaska is the gateway to the Americas for migratory birds coming from Asia, our estimates pertain to the rest of North

<sup>A</sup>Corresponding author. E-mail: winker@alaska.edu

Table 1. Species of waterfowl, shorebirds, gulls, and terns in Alaska with an Old World connection, with estimates of population sizes, proportions, and number of individuals that come to Alaska annually from the Old World. Taxa in bold are Asian; others are shared between the New World and Old World.

Species	Scientific name	AK pop min	AK pop max	% Winter Old World	% Breed Old World	Old World min	Old World max	Source(s)
<b>Family Anatidae</b>								
<b>Tundra bean goose</b>	<i>Anser serrirostris</i>	100 <sup>A</sup>	100	100	100	100	100	Authors
Greater white-fronted goose	<i>A. albifrons</i>	300,000	300,000	0	<10	3000 <sup>B</sup>	30,000	11,24
<b>Lesser white-fronted goose</b>	<i>A. erythropus</i>	10 <sup>A</sup>	10	100	100	10	10	Authors
Emperor goose	<i>Chen canagica</i>	57,500	57,500	<20	>15?	8625	11,500	28
Snow goose	<i>C. caerulescens</i>	80,000	80,000	0	100	80,000	80,000	28
Brant	<i>Branta bernicla</i>	68,100	110,900	1 <sup>C</sup>	5 <sup>C</sup>	681	5545	8
Tundra swan	<i>Cygnus columbianus</i>	142,000	142,000	0	<10?	1420 <sup>B</sup>	14,200	28
<b>Whooper swan</b>	<i>C. cygnus</i>	500 <sup>A</sup>	500	100	100	500	500	Authors
Gadwall	<i>Anas strepera</i>	5000 <sup>A</sup>	5000	0	<10	50 <sup>B</sup>	500	Authors
<b>Falcated duck</b>	<i>A. falcata</i>	50 <sup>A</sup>	50	100	100	50	50	Authors
<b>Eurasian wigeon</b>	<i>A. penelope</i>	1000	1000 <sup>A</sup>	80	100	800	800	Authors
Mallard	<i>A. platyrhynchos</i>	700,000	700,000 <sup>A</sup>	1	5	7000	35,000	7,36
<b>Eastern spot-billed duck</b>	<i>A. zonorhyncha</i>	10 <sup>A</sup>	10	100	100	10	10	Authors
Northern shoveler	<i>A. clypeata</i>	666,000	666,000 <sup>A</sup>	<10	<10	6660 <sup>B</sup>	66,600	7
Northern pintail	<i>A. acuta</i>	905,000	905,000 <sup>A</sup>	<15	<15	45,250 <sup>B</sup>	135,750	7
<b>Garganey</b>	<i>A. querquedula</i>	50 <sup>A</sup>	50	100	100	50	50	Authors
<b>Baikal teal</b>	<i>A. formosa</i>	50 <sup>A</sup>	50	100	100	50	50	Authors
Green-winged teal	<i>A. crecca</i>	713,000	713,000 <sup>A</sup>	1	5	7130	35,650	7,36
<b>Common pochard</b>	<i>Aythya ferina</i>	50 <sup>A</sup>	50	100	100	50	50	Authors
<b>Tufted duck</b>	<i>A. fuligula</i>	500 <sup>A</sup>	500	>90	100	450	500	Authors
Greater scaup	<i>A. marila</i>	900,000	900,000	<10	<10	9000 <sup>B</sup>	90,000	7
Steller's eider	<i>Polysticta stelleri</i>	41,000	41,000 <sup>A</sup>	<10	<10	410 <sup>B</sup>	4100	7,28
Spectacled eider	<i>Somateria fischeri</i>	12,000 <sup>A</sup>	14,000	100	?	12,000	14,000	28
King eider	<i>S. spectabilis</i>	10,000	35,000	53	0?	5300	26,250	27,28
Common eider	<i>S. mollissima</i>	25,500	25,500	1 <sup>C</sup>	5 <sup>C</sup>	255	1275	28
Harlequin duck	<i>Histrionicus histrionicus</i>	170,000	170,000	1 <sup>C</sup>	5 <sup>C</sup>	1700	8500	Authors, 28
White-winged scoter	<i>M. fusca</i>	87,500	87,500 <sup>A</sup>	1 <sup>C</sup>	5 <sup>C</sup>	875	4375	Authors, 7
Black scoter	<i>M. nigra</i>	140,000	140,000 <sup>A</sup>	1 <sup>C</sup>	5 <sup>C</sup>	1400	7000	Authors, 7
Long-tailed duck	<i>Clangula hyemalis</i>	66,000	66,000	1 <sup>C</sup>	5 <sup>C</sup>	660	3300	Authors, 7
Common goldeneye	<i>Bucephala clangula</i>	150,000	150,000	<10	?	1500 <sup>B</sup>	15,000	Authors, 7
<b>Smew</b>	<i>Mergellus albellus</i>	50 <sup>A</sup>	50	100	100	50	50	Authors
Common merganser	<i>Mergus merganser</i>	10,000 <sup>A</sup>	10,000	0	<5	100 <sup>B</sup>	500	Authors
Red-breasted merganser	<i>M. serrator</i>	36,000	36,000 <sup>A</sup>	1 <sup>C</sup>	5 <sup>C</sup>	360	1800	7
<b>Family Charadriidae</b>								
Black-bellied plover	<i>Pluvialis squatarola</i>	50,000	50,000	<15	<15	1000	7500	1, authors
<b>European golden-plover</b>	<i>P. apricaria</i>	10 <sup>A</sup>	10	100	100	10	10	Authors
Pacific golden-plover	<i>P. fulva</i>	35,000	50,000 <sup>A</sup>	0	>20?	500 <sup>B</sup>	10,000	1, authors
<b>Lesser sand-plover</b>	<i>Charadrius mongolus</i>	500 <sup>A</sup>	500	100	100	500	500	Authors
Snowy plover	<i>C. alexandrinus</i>	10	10	100	100	10	0	Authors
<b>Common ringed plover</b>	<i>C. hiaticula</i>	50 <sup>A</sup>	50	100	95	50	50	Authors
<b>Little ringed plover</b>	<i>C. dubius</i>	10 <sup>A</sup>	10	100	100	10	10	Authors
<b>Eurasian dotterel</b>	<i>C. morinellus</i>	100 <sup>A</sup>	100	100	90	100	100	Authors
<b>Family Scolopacidae</b>								
<b>Common greenshank</b>	<i>Tringa nebularia</i>	250 <sup>A</sup>	250	100	100	250	250	Authors
<b>Marsh sandpiper</b>	<i>T. stagnatilis</i>	10 <sup>A</sup>	10	100	100	10	10	Authors
<b>Spotted redshank</b>	<i>T. erythropus</i>	50 <sup>A</sup>	50	100	100	50	50	Authors
<b>Wood sandpiper</b>	<i>T. glareola</i>	500	500 <sup>A</sup>	100	98	500	500	Authors
<b>Green sandpiper</b>	<i>T. ochropus</i>	10 <sup>A</sup>	10	100	100	10	10	Authors
Wandering tattler	<i>T. incanous</i>	20,000	20,000 <sup>A</sup>	0	<10	200 <sup>B</sup>	2000	28, authors
<b>Gray-tailed tattler</b>	<i>T. brevipes</i>	500	500 <sup>A</sup>	100	100	500	500	Authors
<b>Common sandpiper</b>	<i>Actitis hypoleucos</i>	100 <sup>A</sup>	100	100	100	100	100	Authors
<b>Terek sandpiper</b>	<i>Xenus cinereus</i>	50 <sup>A</sup>	50	100	100	50	50	Authors
<b>Little curlew</b>	<i>Numenius minutus</i>	10 <sup>A</sup>	10	100	100	10	10	Authors
Whimbrel	<i>N. phaeopus</i>	24,000	26,000	3	3	720	780	1, authors

Table 1. Continued.

Species	Scientific name	AK pop min	AK pop max	% Winter Old World	% Breed Old World	Old World min	Old World max	Source(s)
<b>Far eastern curlew</b>	<i>N. madagascariensis</i>	25 <sup>A</sup>	25	100	100	25	25	Authors
<b>Black-tailed godwit</b>	<i>Limosa limosa</i>	25 <sup>A</sup>	25	100	100	25	25	Authors
<b>Bar-tailed godwit</b>	<i>L. lapponica</i>	80,000	120,000	100	<15	80,000	120,000	1
Ruddy turnstone	<i>Arenaria interpres</i>	24,000	24,000	10–15	10–15	2400	3600	1
<b>Great knot</b>	<i>Calidris tenuirostris</i>	25 <sup>A</sup>	25	100	100	25	25	Authors
<b>Red knot</b>	<i>C. canutus</i>	50,000 <sup>A</sup>	50,000	0	95	47500	47,500	1
Sanderling	<i>C. alba</i>	3000 <sup>A</sup>	3000	0	<15	30 <sup>B</sup>	450	1, authors
Western sandpiper	<i>C. mauri</i>	3,500,000	3,500,000	0	<10	36750 <sup>B</sup>	351,750	1
<b>Red-necked stint</b>	<i>C. ruficollis</i>	1000 <sup>A</sup>	1000	100	90	1000	1000	Authors
<b>Little stint</b>	<i>C. minuta</i>	25 <sup>A</sup>	25	100	100	25	25	Authors
<b>Temminck's stint</b>	<i>C. temminckii</i>	100 <sup>A</sup>	100	100	100	100	100	Authors
<b>Long-toed stint</b>	<i>C. subminuta</i>	100	100 <sup>A</sup>	100	100	100	100	Authors
Baird's sandpiper	<i>C. bairdii</i>	15,000	45,000 <sup>A</sup>	<5	5?	750	2250	1, authors
Pectoral sandpiper	<i>C. melanotos</i>	150,000	250,000	10?	10?	15,000	25,000	1, authors
<b>Sharp-tailed sandpiper</b>	<i>C. acuminata</i>	8000	48,000	75?	100	6000	48,000	1
Rock sandpiper	<i>C. pilocnemis</i>	150,000	150,000	<20?	<20?	7500 <sup>B</sup>	30,000	1
Dunlin	<i>C. alpina</i>	750,000	1,300,000	54	100	405,000	702,000	1
<b>Curlew sandpiper</b>	<i>C. ferruginea</i>	25 <sup>A</sup>	25	100	99	25	25	Authors
<b>Spoon-billed sandpiper</b>	<i>Eurynorhynchus pygmaeus</i>	10 <sup>A</sup>	10	100	100	10	10	Authors
<b>Broad-billed sandpiper</b>	<i>Limicola falcinellus</i>	25 <sup>A</sup>	25	100	100	25	25	Authors
<b>Ruff</b>	<i>Philomachus pugnax</i>	250 <sup>A</sup>	250	100	99	250	250	Authors
Long-billed dowitcher	<i>Limnodromus scolopaceus</i>	350,000	350,000 <sup>A</sup>	<15	<15	17,500 <sup>B</sup>	52,500	28
<b>Jack snipe</b>	<i>Lymnocyptes minimus</i>	10 <sup>A</sup>	10	100	100	10	10	Authors
<b>Common snipe</b>	<i>Gallinago gallinago</i>	1000 <sup>A</sup>	1000	100	99	1000	1000	Authors
<b>Pin-tailed snipe</b>	<i>G. stenura</i>	25 <sup>A</sup>	25	100	100	25	25	Authors
Red-necked phalarope	<i>Phalaropus lobatus</i>	500,000	1,000,000	<5	?	5000 <sup>B</sup>	50,000	1,28
Red phalarope	<i>P. fulicarius</i>	750,000	750,000	50?	?	375,000	375,000	1,28
<b>Family Laridae</b>								
<b>Black-headed gull</b>	<i>Chroicocephalus ridibundus</i>	50 <sup>A</sup>	250	100	100	50	250	Authors
<b>Black-tailed gull</b>	<i>Larus crassirostris</i>	1 <sup>A</sup>	25	100	100	1	25	Authors
Mew gull	<i>L. canus kamtschatschensis</i>	50 <sup>A</sup>	250	100	100	50	250	Authors
Herring gull	<i>L. argentatus vegae</i>	500 <sup>A</sup>	1000	100	90	500	1000	Authors
<b>Slaty-backed gull</b>	<i>L. schistisagus</i>	250 <sup>A</sup>	500	90	100	250	500	Authors
Glaucous-winged gull	<i>L. glaucescens</i>	500,000 <sup>A</sup>	500,000	<25	<25	5000 <sup>B</sup>	125,000	31, authors
Glaucous gull	<i>L. hyperboreus</i>	30,000 <sup>A</sup>	30,000	20	10	3000	6000	31, authors
Sabine's gull	<i>Xema sabini</i>	30,000 <sup>A</sup>	50,000 <sup>A</sup>	10	10	3000	5000	28, authors
Black-legged kittiwake	<i>Rissa tridactyla</i>	2,500,000 <sup>A</sup>	2,500,000	10	10	250,000	250,000	31, authors
Red-legged kittiwake	<i>R. brevirostris</i>	250,000 <sup>A</sup>	250,000	<20	<1	2500 <sup>B</sup>	50,000	31, authors
<b>Ross's gull</b>	<i>Rhodostethia rosea</i>	500 <sup>A</sup>	2000	100	100	500	2000	Authors
<b>Ivory gull</b>	<i>Pagophila eburnea</i>	500 <sup>A</sup>	1000	50	100	250	1000	Authors
Aleutian tern	<i>Onychoprion aleuticus</i>	10,000 <sup>A</sup>	10,000	100	0	10,000	10,000	31, authors
<b>Common tern</b>	<i>Sterna hirundo longipennis</i>	50 <sup>A</sup>	150	100	100	50	150	Authors
Arctic tern	<i>S. paradisaea</i>	200,000 <sup>A</sup>	300,000	<1	<10	2000 <sup>B</sup>	30,000	28, authors
	<b>MIN &amp; MAX:</b>	15,272,676	16,742,740			1,478,302	2,907,315	
	<b>Anatidae</b>	5,286,970	5,356,770			195,496	593,015	
	<b>Charadriidae</b>	85,680	100,670			2180	18,170	
	<b>Scolopacidae</b>	6,378,125	7,640,125			1,003,475	1,814,955	
	<b>Laridae</b>	3,521,901	3,645,175			277,151	481,175	

<sup>A</sup>Lower/upper limit unknown.<sup>B</sup>Lower limits estimated.<sup>C</sup>Extrapolated assuming that population genetic estimates from two anatid species are representative (36).

America and, for some species, to South America as well. In addition to providing these taxonomic lists and numeric estimates for future modeling and analyses, we examine how the Kilpatrick *et al.* (17) modeling effort might have reached a different conclusion if our data had been available.

## MATERIALS AND METHODS

Avian families likely to be most important as AI virus hosts in this region were determined from the surveillance literature (e.g., 19,23,25). Some bird families that may be important hosts elsewhere, such as rails (Rallidae) and cormorants (Phalacrocoracidae), are in this particular migration system either effectively absent (e.g., Rallidae) or there is no evidence for intercontinental movement (e.g., Phalacrocoracidae) (30). We have omitted Passeriformes, although some have been found to carry HP AI H5N1 (e.g., 20), both because they seem to be ineffective transporters of HP AI (5) and because, while millions of passerines move from Asia to North America, numeric estimates of this part of the Alaska migration system would be very difficult to make.

We developed our list of wild bird AI virus host taxa from several sources (12,13,14,16). We obtained bird abundance estimates from reports (1,7,8,11,24,27,31), Poole and Gill (28), and from unpublished data from the University of Alaska Museum and the authors' field experience. Population genetic data used to infer intercontinental movement rates for two species of ducks were given by Winker *et al.* (36), and these estimates were extended to seven other waterfowl species for which no reliable intercontinental movement rate data are yet available.

Translation of numbers of individual hosts into infectious birds followed Kilpatrick *et al.* (17) with the following changes: These authors used infectious bird days as units of comparison, which they defined thus: number of host individuals  $\times$  virus prevalence rate  $\times$  number of days infected birds shed virus. Due to considerable variation and uncertainties in the last term, both within and among host species (e.g., 6,17,26), we omitted it here and estimated only numbers of infected birds when using the Kilpatrick *et al.* (17) model.

## RESULTS

Fully 33 species of waterfowl (Anatidae), 46 species of shorebirds (Charadriidae and Scolopacidae), and 15 species of gulls and terns (Laridae) are involved in movements from Asia to Alaska (Table 1). Of these 94 species, 11 species of waterfowl, 32 species of shorebirds, and 4 species of gulls and terns are Asian taxa that occur in relatively small numbers in Alaska (Table 1). The remaining species are shared between the Old and New Worlds, and it is among these species that the largest numbers of individuals are moving intercontinentally in this region (Table 1). Although there are clearly gaps in available data, our estimates suggest that among waterfowl (Anatidae) about 195,000–593,000 individuals move from Asia to Alaska each year (Table 1). Among shorebirds (Charadriidae and Scolopacidae), the numbers of individual birds moving between the continents is much higher, approximately 1.0–1.8 million (Table 1). And among gulls and terns (Laridae), approximately 277,000–481,000 individuals appear to come to Alaska annually from the Old World. Altogether, these data suggest that about 1.48–2.91 million individuals in these important host groups move from Asia to Alaska annually (Table 1).

Seasonal variation in AI virus prevalence (e.g., 19) suggests that some seasonal host movements are probably less important than others. We have considered “% wintering Old World” and “% breeding Old World” (Table 1) to help readers and modelers understand at a gross level how a species is moving in this system. For example, greater white-fronted goose (*Anser albifrons*) is a host returning from Asia in autumn (Table 1). Data quality, however, is

insufficient at this time to provide seasonal numeric estimates across this system.

These data provide a host-specific baseline that can be used for improved modeling of AI virus movements between Asia and the Americas. As an example, incorporation of these host movements into the model of AI virus movement given by Kilpatrick *et al.* (17) changes the profile of Asia-to-North-America wild bird hosts in the global spread of highly pathogenic (HP) H5N1. Instead of the low value of approximately four infectious birds calculated for this part of the world's intercontinental waterfowl migration system (Kilpatrick *et al.* (17) online information), our results suggest instead that in waterfowl alone this value is more likely to be 251–761 infectious birds (using prevalence of HP H5N1 among waterfowl from Kilpatrick *et al.* (17) of 0.0012837 and multiplying this value by the Old World min-max values in Table 1 for Anatidae). For HP AI modeling like this it may be warranted to restrict models to waterfowl; however, even at very low prevalence rates the sheer numbers of hosts involved in other families (e.g., Scolopacidae, Table 1) argue for consideration. For general AI modeling (LP and HP) among all of the host groups we consider relevant for AI virus movement in this region (waterfowl, shorebirds, and gulls and terns), thousands of infectious birds may be involved in annual Asia-to-America migrations (1898–3732 individuals if using the same prevalence rate from Kilpatrick *et al.* (17)). We caution that these estimated values depend on prevalence rates and strain-specific attributes (if not being used for overall AI movement estimates), but our study shows the effects of incorporating more specific data into AI movement models in this region. In general, it is clear that, for heuristic value, multiplying these host numbers by any small constant (i.e., infection prevalence) shows that the numbers involved are relatively large. Importantly, host availability in Alaska once these intercontinental vectors arrive is also very high, representing at least 5–10 times more birds and infectious birds (the latter important as possible “mixing vessels” for viral reassortment) than the vector populations moving from Asia to North America (Table 1). Note that these data do not include North American host species whose ranges do not extend to Asia, and they do not include continental populations outside of Alaska; thus the total recipient host population is even larger.

## DISCUSSION

Alaska's interconnectedness with distant places through migratory birds is remarkable. Birds breeding in Alaska during the boreal summer spend the boreal winter on fully six continents: Asia, Australia, Antarctica, Africa, South America, and elsewhere in North America. Four of these continents make Alaska an important nexus of intercontinental connectivity for AI virus movement through its migratory birds: Australia (including New Zealand), Asia, North America, and South America. Birds wintering in Australasia and Asia and breeding in Alaska provide a widespread geographic source of potential viruses from lands and waters of the western Pacific, whereas birds that breed in Alaska (and/or eastern Asia) and winter elsewhere in North America and South America provide suitable hosts for spreading these viruses across the Americas. Of course, the opposite is true as well. The waterfowl and shorebirds involved in direct intercontinental movements through Alaska (Table 1) represent only a portion of the taxa suitable to spread incoming viruses widely across the Americas following cross-species and cross-continental AI infections. Our analyses focus only on the “out of Asia” aspect of this migration system. Once into Alaska, the numbers of suitable migratory hosts are much higher, as Table 1

shows only for those taxa with intercontinental movements. When American hosts from other destinations are considered (e.g., Canada, the lower 48 U.S. states, Middle and South America), the numbers of suitable hosts are much higher.

Precisely how AI viruses move within this dynamic and complex system remains to be fully understood. Here we have focused on the host movement system rather than on the viruses themselves so that as knowledge of the latter improves, a relatively accurate host-specific baseline can be incorporated into AI virus movement models that include this region. We are not advocating any specific modeling approach, nor are we focusing on specific subtypes or strains of AI, although we recognize that future modelers will likely wish to do so; our goal has been to provide more accurate data on the relevant host system. Ecological and host-physiological differences between HP and LP AI viruses are complex phenomena beyond the scope of this paper. Pathogenicity, however, is defined by virus effects in chickens, and it is a strain-specific evolutionary threshold (in relation to one host species), not a monophyletic subset of AI viruses. Pathogenicity varies among host species (e.g., 3,6,15,35), among individuals within species (e.g., 26), and within virus lineages and subtypes, and the spread of LP viruses is important in occasionally producing HP viruses, primarily in intermediate hosts (33). Even the currently circulating HP H5N1 may have sufficiently low pathogenicity in some duck species to enable them to be effective long-distance vectors of this disease (15). Thus, different virus strains are likely to have differential effects and movement propensities among the different host species in this migration system. Our point is that it is important when modeling the spread of AI viruses to consider the scope of the major host groups carrying LP and HP AI strains; the scope we provide can be narrowed as warranted, depending on exactly what is being modeled. This wild bird reservoir can provide the virus genes for the next epidemic in humans or epizootic in animals and thus poses an ongoing risk.

In their models of the spread of H5N1 from Asia to North America, Kilpatrick *et al.* (17) only included migratory waterfowl from Asia that reach the contiguous 48 U.S. states in winter, but their data in this regard were incomplete; the northern pintail (*Anas acuta*) alone, for example, exceeds their total estimate for this migration system (Table 1; see also Miller *et al.* (22)). Furthermore, Kilpatrick *et al.* (17) neglected to include the numerically dominant AI host group in this region, the shorebirds (Charadriidae and Scolopacidae, Table 1), in which many AI hemagglutinin (HA) subtypes occur, including H5s (19), and in which H5N1, the focus of their model, has also been reported (9). HP H5s have also been reported in the family Laridae (e.g., 2,9,21). We thus consider it appropriate to include more of the relevant taxa on the North American continent, because of the rich recipient host populations in Alaska (Table 1 plus species without intercontinental movements in this region), clear AI virus links between Alaska and the lower 48 U.S. states (32), and evidence of intercontinental transport of LP AI viruses in this region (18). We recognize that Anatidae is probably the most important family for AI transport and that others are likely less relevant, but that relevance is not zero (e.g., 2,9,19,21), especially considering the numbers of animals involved (Table 1).

Using the model of Kilpatrick *et al.* (17), a reevaluation based on our more accurate host number estimates reverses the ratio of risk between domestic and wild bird movements into the U.S. from 25.5–255:2 infectious bird days given by Kilpatrick *et al.* (17; their Fig. 2) to 12.7–127:251–761 infectious birds in waterfowl alone (the taxonomic limit of their modeling), or to perhaps as much as 12.7–127:1898–3732 among all host groups considered here (from Kilpatrick *et al.* (17) online information). Note that we have

converted units by eliminating the uncertain values of number of days that infected birds shed virus to focus more directly on host numbers; this does not affect the reversal of the ratio of risk. Also, in extending their model to other host groups we used their same prevalence rate, which seems unlikely but which only further fieldwork can determine. Based on our incorporation of more accurate numbers of waterfowl hosts alone, this revised model would change the conclusions of Kilpatrick *et al.* (17), suggesting instead that introduction of the HP H5N1 into the United States is more likely to occur directly from wild birds rather than indirectly, first into the New World through the poultry trade and secondarily into the United States through migratory birds. We note, however, that the Kilpatrick *et al.* (17) estimates of total poultry trade values (number of infectious bird-days) for the entire Western Hemisphere do exceed our estimates of direct Asia-to-America wild bird host movements, so their conclusion that the poultry trade is more likely to introduce the highly pathogenic H5N1 into the New World likely remains valid. Nevertheless, migratory birds clearly play an important role.

We emphasize that our point here is not *how* one models AI virus movements, but that a more complete consideration of intercontinental host movement is required. As Yasué *et al.* (37) suggested, better ecological data and greater interdisciplinary participation are needed to understand the epidemiology of avian influenza viruses. Anthropogenic movements of avian hosts through the poultry and the captive bird trades can be regulated. Wild bird movements cannot. A full accounting of the wild bird hosts involved in intercontinental and long-distance movements is a critical first step in understanding their role in global AI virus movements. Our results (Table 1) should help in defining the key taxonomic, geographic, and seasonal factors involved in this complex intercontinental association of wild bird AI hosts. The next steps are to determine infection rates of LP and HP viruses among these hosts and to incorporate these into dynamic models.

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